

## NOTE

# Achiasmy or heterochiasmy: Does meiotic recombination occur in female Lepidoptera?

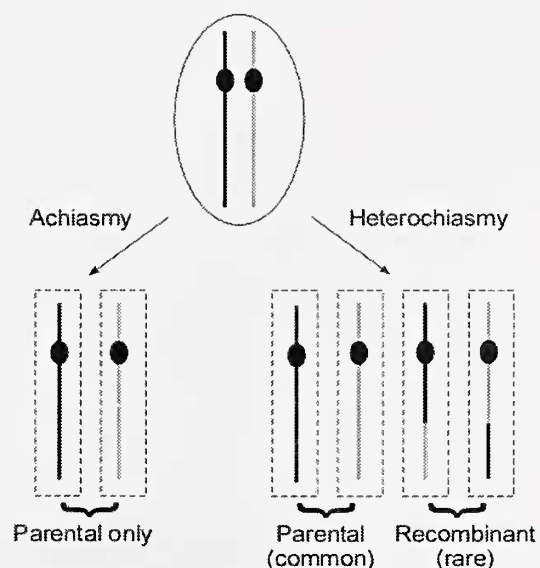
Sexual dimorphism in the amount of crossing-over and recombination during gamete formation (meiosis) is common in insects (Trivers, 1988; Burt *et al.*, 1991). In many cases, recombination in the different sexes differs not only on sex chromosomes but also on autosomes. In *Drosophila*, for example, genetic exchange between homologous chromosomes is completely absent in males (Morgan, 1914). This phenomenon, called “achiasmy,” occurs frequently in Diptera, and in several other insect orders including Lepidoptera (Bell, 1982). According to the Haldane-Huxley rule (Haldane, 1922; Huxley, 1928), when one sex has achiasmate meiosis, it is always the heterogametic sex (XY or WZ). Lepidoptera have WZ/ZZ sex determination; therefore, females, not males should be achiasmate.

Meiotic recombination in Lepidoptera has been studied for decades, and female achiasmy has been found in several Lepidoptera species (Suomalainen *et al.*, 1973; Turner & Sheppard, 1975; Scriber *et al.*, 1995; Heckel *et al.*, 1999). Consequently, the absence of meiotic recombination in females is thought to be a general phenomenon of all butterflies and moths. The pivotal evidence for Lepidoptera achiasmy comes from classical cytogenetic and genetic breeding studies. Advanced cytogenetic imaging techniques have recently been applied to obtain improved and more convincing results (Marec & Traut, 1993; Yoshido *et al.*, 2005). In female meiosis, synaptonemal complexes appear to be modified and are fundamentally different from chiasmata found in males (Marec & Traut, 1993). The absence of normal chiasmata at oogenesis is believed to prevent crossing-over in female butterflies and moths.

Perhaps surprisingly, genetic studies by Carter and Watt (1988) and Wang and Porter (2004) both

showed the presence of crossing-over in female *Colias* butterflies. The amount of recombination, however, is considerably less than that in males, with the ratio of female-to-male map length being approximately one third (Wang & Porter, 2004). This situation is called “heterochiasmy” (see Figure 1 for an illustration of the difference), in which both sexes recombine, but with quantitative differences in frequency. Similar to the phenomenon of achiasmy, heterochiasmy tends towards less recombination in the heterogametic sex (Trivers, 1988), which was confirmed by the study of *Colias* butterflies.

Early karyological studies of a few Lepidoptera species, though ambiguous, indicated that chiasmata might actually form in bivalents at oogenesis (reviewed by Robinson, 1971, also refer to Table 1 for a summary). These “exceptional chiasmata,” which were documented in the silkworm, appear to occur rarely (Maeda, 1939). It has also been determined



**Figure 1.** Schematic sketch of gamete formation in female Lepidoptera, illustrating the processes involving achiasmy vs. heterochiasmy. For simplicity, only one pair of chromosomes is shown. In the case of achiasmy, all meiotic products (gametes) are parental type, while gametes of recombinant type are present in the case of heterochiasmy.

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**Table 1.** Observed cases of heterochiasmy in Lepidoptera.

Species	Evidence	Recombination frequency of females	References
Some race of <i>Bombyx mori</i>	karyological observations	0.36%	Maeda, 1939
<i>Trichiura crataegi</i>	microphotographs of chiasmata	unknown	Federley, 1945
<i>Thera obeliscata</i> and <i>T. variata</i>	karyological study of the bivalent structures	unknown	Suomalainen, 1953
<i>Philosamia ricini</i>	karyological studies	unknown	Srivastava & Gupta, 1962
<i>Colias eurytheme</i> and <i>C. philodice</i>	genetic mapping	1/3 of the frequency of males	Carter & Watt, 1988; Wang & Porter, 2004

that the two sexes of Lepidoptera differ markedly in the number as well as in the position of chiasmata. In females, crossing over is likely to arise only at the ends of the bivalents and terminate shortly thereafter (White, 1954). As a result, recombination is greatly reduced and confined to small chromosomal areas. This is consistent with the results of mapping studies of *Colias* butterflies, where genetic markers clustered in the middle of the linkage groups and longer gaps appeared near the ends (Wang, 2005).

Therefore, the generally held view of female achiasmy in Lepidoptera is not entirely accurate, because, at least for some species, crossing-over is not completely suppressed. Clearly, there is variation in female recombination rates among different Lepidoptera species, some being achiasmatic and others heteroachiasmatic. Such variations may be explained by sex differences in gene epistasis, sexual selection, or gamete selection (Lorch, 2005; Lenormand & Dutheil, 2005). Heterochiasmy is hard to detect and differentiate from achiasmy because the crossing-over events are rare and largely confined to small regions of the chromosomes. The known incidence of heterochiasmy in Lepidoptera may increase as further studies provide a greater understanding of sexual dimorphism in autosomal recombination.

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